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FECUNDITY OF NORTH AMERICAN SALMONIDAE

By GEORGE A. ROUNSEFELL

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ABSTRACT

Data on fecundity of North American Salmonidae are scarce, but analysis of available material shows that use of the total number of females as a measure of reproductive potential may introduce considerable error. Fecundity varies between populations of the same species, so that data from one locality cannot be safely applied to another. Annual differences in fecundity in the same population may be caused by differences in average size, or by differences in age at maturity.

Fecundity in the sockeye does not appear to vary between fish remaining for 3 or 4 years in the lake before seaward migration, but fish spending 2 years at sea have a higher fecundity than fish of the same size spending 3 years at sea.

Data are needed to answer two questions: (1) What is the relation between egg size and egg number in the same species; and (2) Does reproductive potential depend chiefly on number of eggs or on total volume of eggs.

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FECUNDITY OF NORTH AMERICAN SALMONIDAE

By George A. Rounsefell, *Fishery Research Biologist*

This paper is the first in a projected series in which the author proposes to compile and evaluate the published information on various phases of the life history and conservation of North American salmonids. The available information is so widely scattered that merely bringing it together will facilitate the expanding research. Furthermore, even a hasty perusal of the literature reveals large gaps in our knowledge. Once these gaps are clearly seen, there is a much better chance of their being filled.

The primary purpose, however, is to discover through comparison of the same life phases of the different species and genera, the relation between the fish and the ecological factors in their environment. Since emphasis has been placed on material that would aid in developing principles, and as I am making the study as complete as possible without assistance, I am not including minor items of information. Original data are presented for Karluk River sockeye.

Although not indigenous, the brown trout, *Salmo trutta*, is included in this study as a thoroughly naturalized species. European and Asiatic literature is used sparingly, either to aid where knowledge of the North American stock is deficient, or to corroborate the North American findings.

Fecundity is an especially interesting topic in the Salmonidae because the comparatively small number of large eggs suggests (as other researchers have proved, e. g., Rounsefell and Kelez, 1938, Rounsefell, 1949 and in ms.[1]) a demonstrable relation between the reproductive potential of the spawning stocks and the numbers of young surviving. Neave (1948) has also pointed out that the variation in egg number between species of *Oncorhynchus* is related to the varying vicissitudes of their life history.

The relation between size of spawning stock and number of young produced is fundamental to studies of changes in population size. The survival from spawnings cannot always be determined at an early stage, but is more usually measured at some later stage of the life history. In this paper we are concerned with quantitative measurement of the reproductive potential of the spawning stock. Such measurements are usually gross estimates derived from one of the following bases:

1. Relative abundance of the adult population. This will usually be in pounds of fish caught by some standard amount of fishing effort (a standardized unit of gear fishing a certain period of time).

2. Relative abundance of the eggs or larvae. This usually is a summation of the density of eggs (in the case of pelagic eggs) per cubic meter over the water area inhabited by the particular population under consideration. Estimates of abundance of species spawning in the littoral zone, e. g., Pacific herring (*Clupea pallasi*), may be based on miles of shoreline utilized for spawning.

3. Actual numbers of mature adults. These numbers may be an actual count of the individuals or may be statistical estimates of population size.

These measures of reproductive potential are each based on one or more of the following assumptions:

1. That the number of eggs spawned is in direct proportion to the number of mature adults and their mean weight (or length). For this to be true, the relation between size of fish and fecundity must be linear. Moreover, if the size composition of the adult population varies from year to year, then the theorem is true only if the regression of eggs on size passes through the origin, i. e., the regression formula must be of the form $y=bx$.

[1] Factors causing decline in sockeye salmon of Karluk River, Alaska. U. S. Department of the Interior, Fish and Wildlife Service, Washington, D. C.

Approved for publication, February 8, 1957.

2. That the annual sex ratio remains constant.
3. That the regression of number of eggs on size of fish does not vary between years.
4. That the size and/or age at maturity does not vary between years.
5. That the number of eggs is a function of fish size independent of age.
6. That there is no annual variation in the proportion of the eggs retained by the females in spawning.

The foregoing assumptions are usually not fully satisfied so that the variability of an approximate measure of reproductive potential in critical experiments may be so large as to obscure the very factors, the effects of which the biologist is seeking to measure.

This variability between numbers of mature adults and actual reproductive potential has long been recognized, and biologists have attempted to discount it by substituting an estimation of the total annual egg deposition for number of adults as being a better measure of reproductive potential. This paper is confined to an analysis of the factors causing variation in the relation between number of eggs and number of mature adults.

After making the necessary allowance for differences in size of fish, a wide range in fecundity still exists between races of the same species from different localities. For instance, McGregor (1922, 1923a) found that the king salmon of the Sacramento River have a far higher fecundity than those of the Klamath River. Thus, if y is number of eggs and x is length of the fish in centimeters, the formulae for the regressions of number of eggs on length are—

Klamath River ..... Log $Y=.00682\ X+3.01116$
Sacramento River ..... Log $Y=.00319\ X+3.56836$

The Klamath River fish (65 specimens) ranged from 61 to 107 centimeters in length (average, 82.6), with a geometric mean of 3,754 eggs. The Sacramento River fish (50 specimens) ranged from 59 to 110 cm. (average, 92.4) and had a geometric mean of 7,298 eggs. At 85 cm., the calculated geometric means for the two populations are 3,894 and 6,912 eggs, an increase of 78 percent in number of eggs for the Sacramento River fish when compared with king salmon from the Klamath River.

The question arises as to the causes and the biological significance of such a great difference i fecundity between populations of the same specie It is recognized that harsher ecological situatio impose lower survival rates on some race Assuming that the number of eggs can be in creased by selection (as seems to have been don for domesticated strains of trout), then th number of eggs may well differ genetically betwee various wild races of salmonids. In the case i point there is good reason to believe that th variation in egg number is not caused by variatio in the marine environment since, as McGreg pointed out (1923b), Sacramento River an Klamath River king salmon occur together in th ocean troll catches.

That the fecundity of fish of the same leng may even differ widely between populatio spawning in different portions of the same riv system is shown by Aro and Broadhead (195 for the sockeye salmon of the Skeena Rive For 3 years, 1939, 1948, and 1949, the fema sockeye of small Lakelse Lake (5.5 sq. m averaged 58.9 cm. in length (58.1–59.6) with a average of 3,816 eggs (3,699–3,888); while for t 3 years of 1946, 1947, and 1949, the female socke of the large upriver Babine Lake (171.8 sq. m averaged 58.5 cm. (57.1–60.1) in length with a average of only 3,181 eggs (3,056–3,389).

In assessing the significance of differences fecundity between fish of various localities, becomes important to measure the variation with localities. Some of the important factors with localities to be considered are—

1. Size of the fish in relation to number eggs.
2. Age at maturity.
3. Size of the eggs.
4. Seasonal trends in fecundity in the sa locality.
5. Annual variation in fecundity.

RELATION OF SIZE OF FISH TO NUMBE OF EGGS

Combining his own observations with those Titcomb (1897), Ricker (1932) states that t relation between number of eggs and length fish is curvilinear for the eastern charr, or bro trout, *Salvelinus fontinalis*. The number of eg varied from 80 in a 5.1-inch charr to 5,630 i 22-inch charr. However, Allen (1956) points o

that Titcomb's data are of limited value since Titcomb stated that some of the charr had apparently dropped part of their eggs before being captured. Osgood Smith (1947) obtained a linear relation between the logarithm of the number of eggs and the body length of 29 eastern charr, but inasmuch as his specimens were from such diverse localities as California, Ontario, and North Carolina, the results cannot be regarded as conclusive.

The number of eggs of eastern charr from four localities is shown according to size of fish in table 1 and figure 1. These data show that the differences in egg number between localities are too great to permit combining localities in studying the egg number–fish size relation. When the curves for the separate localities are examined, it becomes apparent that the number of eggs increases approximately as the weight of the fish, since the logarithm of egg number plotted against the logarithm of fish length approximates a straight line, as does the logarithm of fish weight against the logarithm of fish length.

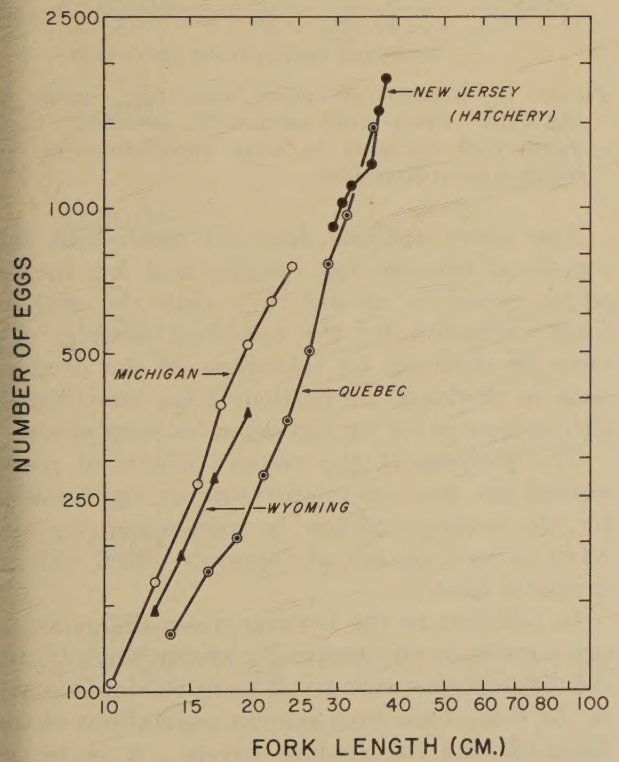

FIGURE 1.—Relation of egg number to body length in *Salvelinus fontinalis.*

TABLE 1.—*Fecundity of eastern charr,* Salvelinus fontinalis

Locality and fork length	Number of fish	Average number of eggs	Authority
Wyoming (beaver pond):			
12.70 cm	2	148	Allen (1956).
14.44 cm	5	191	
16.82 cm	5	275	
19.65 cm	2	376	
New Jersey (hatchery stock):			
29.69 cm [1]	5	916	Hayford and Embody (1930).
31.00 cm	4	1,028	
32.13 cm	30	1,114	
35.21 cm	22	1,249	
36.50 cm	4	1,611	
38.00 cm	8	1,867	
Michigan (streams):			
10.40 cm [2]	38	104	Cooper (1953).
12.73 cm	91	169	
15.07 cm	59	268	
17.41 cm	24	395	
19.74 cm	15	525	
22.08 cm	8	643	
24.42 cm	4	753	
Quebec (Laurentides Park):			
13.75 cm	4	131	Vladykov and Legendre (1940).
16.25 cm	14	177	
18.75 cm	10	206	
21.25 cm	11	280	
23.75 cm	14	362	
26.25 cm	13	505	
28.75 cm	3	732	
31.45 cm	6	970	
35.50 cm	2	1,469	

[1] Converted from standard length by factor 1.1.
[2] Converted from total length by factor 0.92.

The logarithm of the number of eggs shows a closer linear relation to length than does the actual number of eggs when specimens are available over a wide range of length. However, over the rather narrow ranges of length at maturity found in *Oncorhynchus,* the difference is usually trifling and can be disregarded in computing.

Extensive data on the relations between number of eggs and length and weight of the fish are given by Foerster and Pritchard (1941). Correlations between egg number and fish length and between egg number and fish weight are shown for Cultus Lake sockeye for each of 6 years (1932–35, 1937, and 1938) and for pink salmon from McClinton Creek, Masset Inlet, for each of 6 even-numbered years from 1930 to 1940, inclusive.

In order to compare the values of the two series of correlations, we have combined the correlation coefficients for the various years by transforming the r values into z values (Fisher 1930, p. 171). The value of r for the combined samples is obtained from the weighted average value of z. The results are as follows:

	Value of correlation of egg number with—	
	Fish length	*Fish weight*
Sockeye salmon (Cultus Lake)	0. 57	0. 56
Pink salmon (McClinton Creek)	0. 35	0. 40

This means that in the sockeye about 31 to 32 percent of the variation in number of eggs is

associated with change in length of the fish; but in the pink salmon this association is much weaker, only about 12 to 16 percent.

The two combined regression lines for number of eggs on length and on weight of the fish in figures 3 and 4 of Foerster and Pritchard (1941, pp. 58, 59) obviously have much steeper slopes than the regressions for the individual years, showing that these lines do not represent the regressions within years. Since the mean annual lengths of the fish varied in the same direction as the average number of eggs, these combined lines represent chiefly regression between years and are therefore of no utility in predicting egg number for various fish lengths within any individual year.

As the relation between egg number and fish length within any year appears to be so weak in pink salmon, it is of interest to determine what factor is controlling egg number. One factor for which measurements are available is sea temperature at Ketchikan, Alaska, which is just across Dixon Entrance from Masset Inlet and slightly east of it. To determine the role of sea temperature we have made a covariance analysis using the pink salmon data from McClinton Creek, Masset Inlet, B. C., prepared by Foerster and Pritchard (1941), as follows:

Year	Mean length (X_1)	Mean sea temperature in degrees Fahrenheit at Ketchikan, July to Sept. (X_2)	Mean number of eggs (Y)
	Cm.		
1930	51.1	56.7	1,535
1940	51.6	57.0	1,619
1938	52.7	55.3	1,698
1934	53.0	55.4	1,804
1936	53.0	54.8	1,899
1932	54.0	54.9	1,758
Average	52.67	55.68	1,719

The results of the test are as follows:

Number of eggs (Y)	Fish length (X_1)	Sea temperature (X_2)
Correlations of Y with X's	0.7801	−0.8592*
Standard regressions of Y on X's	0.0310	−0.8314*

R=0.8593 (N. S.)
Y=3.834X_1−115.616X_2+7,954
Standard error of β's=0.21536

t for $\beta_{Y2.1}$=0.83138/0.21536=3.860
P of .05 =3.182.

The relation between the average number of eggs in McClinton Creek pink-salmon females and the summer sea temperature at Ketchikan, with fish length held constant, is shown in figu 2. The correlation, r_{12}, of X_1 with X_2 is −0.90 and is statistically significant. Obviously, bot annual mean fish length and annual mean eg number are negatively correlated with sea tem perature. The annual differences in mean eg count in pink salmon are a function of sea tem perature, because it is the principal factor co trolling average fish length.

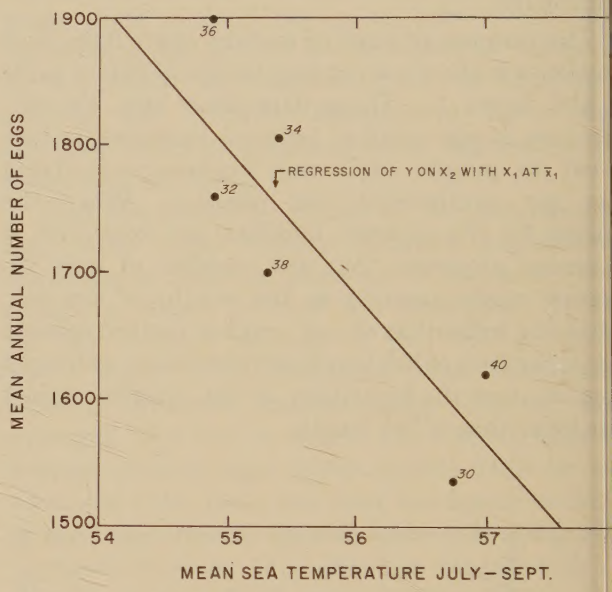

FIGURE 2.—Relation of annual mean egg number McClinton Creek pink salmon, *O. gorbuscha*, (boc length held constant) to mean July–September s temperature at Ketchikan.

The above analysis does not mean that th regression between egg number and fish lengt within years is invalid, but that the within years regression for the combined samples ca only be obtained by reanalysis of the origin data to eliminate the portion of the total regre sion accounted for by regression between years.

The problem of the relative effects of mea annual size and sea temperature on egg numb for the sockeye salmon is complicated by th effect of varying age at maturity which will b discussed later.

In addition to the between-years difference i egg number at any particular length, there is als the difference between rivers mentioned previousl in the case of the king salmon populations of th Klamath and Sacramento Rivers. A better i lustration of this is perhaps afforded by the dat from Eguchi, Hikita, and Nishida (1954) on chu

salmon, *Oncorhynchus keta*, in Japanese waters. They point out that chum salmon from Hokkaido rivers have a larger number of eggs than chum salmon from rivers in South Kurile; however, analysis of their data shows that in both areas there is a significant difference between individual rivers. The analysis, based on data from 7 rivers in Hokkaido and 109 specimens of chum salmon, is as follows, using data for the left ovary only to simplify the tabulations:

Source of variation	D. F.	Sums of squares and products			Errors of estimate		
		Sx^2	Sxy	Sy^2	Sums of squares	D. F.	Mean square
Total	108	2250.0300	64603.0	6, 992, 007	5, 137, 112	107	
Between rivers	6	666.0752	28678.8	2, 369, 067			
Within rivers	102	1583.9548	35924.2	4, 622, 940	3, 808, 177	101	37, 704.7
For test of significance of adjusted means					1, 328, 935	6	221, 489.2

$F=221,489.2/37,704.7=5.87$. For P of .01, $F=2.99$

Similarly for South Kurile rivers, $F=3.50$ with F for P of .01 of 3.17. For the combined data (243 specimens) which come from 13 rivers, $F=13.74$ with F for P of .01 of 2.27. This shows that there is a tendency for each river to have its own regression line for egg number on fish length.

The fact of differences between the regressions for chum salmon from different rivers results in three regression lines (three center curves of figure 3). The total regression (dotted line)

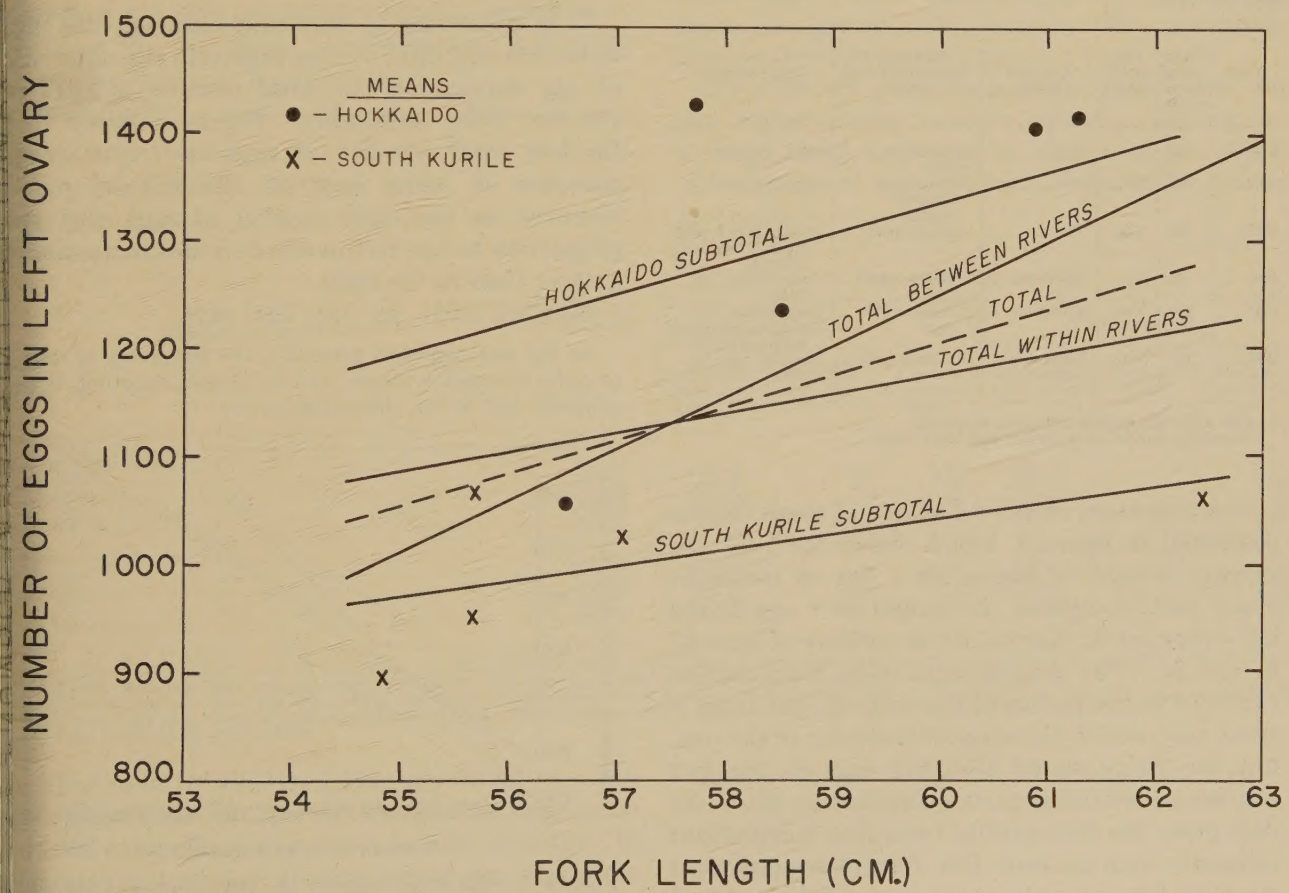

FIGURE 3.—Relation of egg number (left ovary) of Japanese chum salmon, *O. keta*, to body length to illustrate total, between-rivers, and within-rivers regressions.

includes both the within- and the between-rivers regressions. The within- and the between-rivers regressions each has a useful connotation. If one wishes to estimate from the lengths of the fish, the number of eggs contained in a sample of chum salmon from a particular river, then from the between-rivers regression one obtains an estimate of the average number of eggs per female (left ovary) in accordance with the average length of the entire sample. If, however, one wishes to determine the difference in egg number (left ovary) between fish of different lengths within the same sample, then the slope of the regression would follow the within-rivers slope.

RELATION OF AGE AT MATURITY TO NUMBER OF EGGS

The best material available on the effect of age at maturity on egg count is in unpublished data for the sockeye salmon of Karluk River, Alaska, as follows:

Year	Number of specimens	Ages available	Lengths taken	Method of enumeration of eggs [1]	Dates sampled
1926 [2]	40	No	Yes	Number in 5 gm.	Sept. 15, 1926.
1938	65	Yes	Yes	Weight of a counted sample.	Aug. 1–6, 1938.
1939	220	Yes	Yes	Actual count	June 9–July 6, 1939; no dates for individuals.
1940	155	Yes	All 60 cm.	Volume—200 eggs.	June 2–Sept. 13, 1940.
1941	114	Yes	All 60 cm.	Volume—200 eggs.	June 9–Sept. 8, 1941; no sampling July 3–Aug. 11.
1943	182	No	Daily average.	No information.	June 29–Aug. 18, 1943.

[1] Left and right ovaries estimated separately.
[2] Summary published in Gilbert and Rich (1927).

Some measure of the reliability of these data is contained in figure 4, which shows for 1938 the average weight in grams for 1 egg of the right ovary plotted against the weight of 1 egg of the left ovary for 41 Karluk River sockeye of ages 5_3, 6_3, and 6_4. The samples were taken from salmon captured at the mouth of the river so that there is great variation in the stage of maturity of the ova, but the figure shows that the eggs in the two ovaries are maturing at the same rate. Since the data from the two ovaries form two independent estimates from the same fish, their close agreement gives confidence in the consistency of this method of calculating the number of eggs.

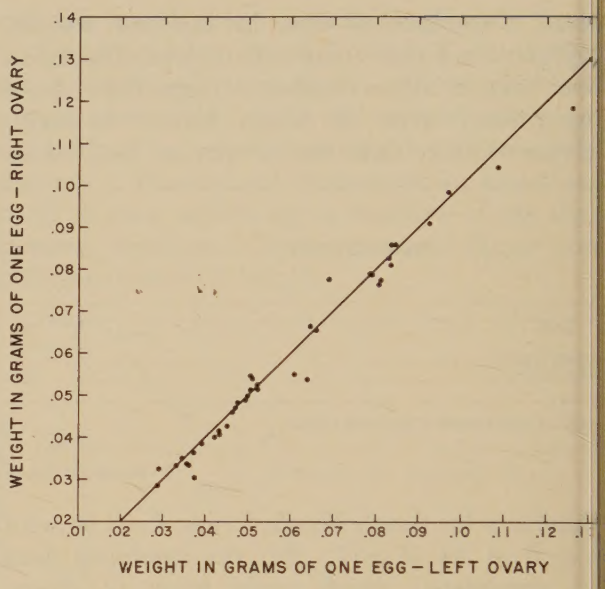

FIGURE 4.—Paired observations of egg weights in right a left ovaries of sockeye salmon, *O. nerka*, of ages 5_3, and 6_4, of Karluk River in 1938.

It is interesting to note that although the eg in the left and right ovaries maintain the same ra of egg maturation the total number of eggs the two differ noticeably. Figure 5 shows th for low total number of eggs the right ova contains as many eggs as the left or mo however, as the total number of eggs rises t proportion in the left ovary becomes increasing greater than in the right.

Kendall (1921, pp. 195, 197) says,

As the ova approach maturity, the left ovary is nea or quite always the longer, and it extends, tapering, to posterior end of the abdominal cavity.

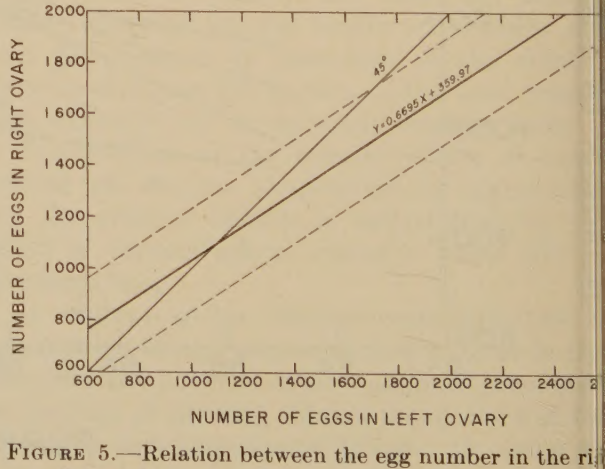

FIGURE 5.—Relation between the egg number in the ri and the left ovaries of the sockeye, *O. nerka*, of Kar River in 1939.

These backward extensions of the ovaries are formed by the maturing and enlarging ova filling the previously crowded interlamina spaces at the posterior end of the ovary, thus stretching it longitudinally.

This increasing disproportion between the left and right ovaries in fish with larger numbers of eggs is logical since in a fish with few eggs the posterior portion of the body cavity would be relatively empty. Fish of the same size with more eggs would have to utilize this space and the left ovary, which is usually longer than the right, would thus be proportionately larger. However, for the chum salmon in Japanese waters, the data of Eguchi et al. (1954) show no significant differences in egg number between the two ovaries. For 243 chum salmon the averages are 1,134 in the left ovary and 1,146 in the right ovary. Sockeye salmon from little Bare Lake in the Red River system of Kodiak Island contain more eggs in the right than in the left ovaries (personal communication from Philip R. Nelson). It is interesting to speculate whether this is a genetic difference or induced by the great environmental difference between Bare and Karluk Lakes.

Probably the best explanation of this disproportion in the size of the two ovaries is given by Brown and Kamp (1942, p. 196). In discussing the brown trout, *Salmo trutta*, they say—

> In the brown trout, the posterior portion of the intestine usually bends strongly to the right, thus crowding the right ovary at its caudal end. The length of the ovary is inversely proportional to the degree of crowding. However, the left ovary is not always the longer. One fish was observed to have a longer right ovary and it was interesting to note that this specimen had an intestine which bent to the left instead of the right. In one or two fish the ovaries were of approximately equal length, with the intestine bending neither to the right nor the left.

They found in 8 brown trout averaging 36 cm. in standard length that the right ovary was 133 mm. long and weighed 32.4 grams, while the left ovary averaged 169.5 mm. and weighed 42.6 grams.

In discussing the effect of age at maturity on number of eggs in *Oncorhynchus* there are two questions: (1) Is the number of eggs determined by length of residence in fresh water or length of residence in the sea? (2) Does the number of eggs for any given length of fish increase or decrease with age? These questions cannot be answered by the pink salmon data because they leave fresh water immediately after emerging from the gravel, and because they invariably mature in their second year.

The following tabulation has been made for the Karluk River sockeye salmon, showing the average number of eggs in relation to the period of residence of the salmon in fresh water and in the ocean.

Ocean age and year sampled [1]	Summers in ocean	Fresh-water age [2]					
		In third year			In fourth year		
		Summers in fresh water	Number of fish	Average number of eggs	Summers in fresh water	Number of fish	Average number of eggs
2-year ocean age:							
1938	1936–37	1934–35	24	3,430	1933–35	10	2,972
1939	1937–38	1935–36	36	3,055	1934–36	7	2,674
1940	1938–39	1936–37	80	3,421	1935–37	25	3,549
1941	1939–40	1937–38	45	3,708	1936–38	36	3,668
3-year ocean age:							
1938	1935–37	1933–34	9	2,631	1932–34	[3] 2	3,610
1939	1936–38	1934–35	58	2,973	1933–35	13	2,866
1940	1937–39	1935–36	23	2,926	1934–36	1	3,459
1941	1938–40	1936–37	20	3,011	1935–37	11	3,160

[1] Since smolts enter the sea from early to late spring and reenter the rivers as adults from spring to early fall the ocean age gives number of ocean summers, but 2 years at sea may vary from about 23 to 27 months. The growing seasons are of paramount importance to this discussion.
[2] Fresh-water age is from the time the eggs are deposited (from late June to November) until smolts enter the sea (from May to July), so that a fresh-water age of 3 can vary from about 29 to 36 months in fresh water, but the summers spent in the lake after hatching are the periods important to this discussion.
[3] Not corrected for length of fish.

The data for 1940 and 1941 are for 60-cm. fish, so to make the data for 1938 and 1939 comparable to data for the other years it was necessary to obtain the number of eggs for 60-cm. fish from the regressions of eggs on length of fish. These regressions were computed separately for the left and the right ovaries and the counts for each, calculated from these regressions, were then combined.

In order to discount environmental effects the

averages were compared according to seasons spent in each environment as follows:

Summers in lake	Ocean age				Difference
	2-year		3-year		
	Number of fish	Average number of eggs	Number of fish	Average number of eggs	
1934–35	24	3,430	58	2,973	457
1935–36	36	3,055	23	2,926	129
1936–37	80	3,421	20	3,011	410
1933–34–35	10	2,927	13	2,866	106
1935–36–37	25	3,549	11	3,160	389
Average		3,285		2,987	[1] 298±74.7

Summers in ocean	Fresh-water age				Difference
	3-year		4-year		
	Number of fish	Average number of eggs	Number of fish	Average number of eggs	
1936–37	24	3,430	10	2,972	458
1937–38	36	3,055	7	2,674	381
1938–39	80	3,421	25	3,549	−128
1939–40	45	3,708	36	3,668	40
1936–37–38	58	2,973	13	2,866	107
1938–39–40	20	3,011	11	3,160	−140
Average		3,266		3,148	118±103.7

[1] t—3.99, P for 0.05=3.75, 4 d. f.

The significant difference of 298 eggs between fish spending 2 summers at sea and those spending 3 summers, but with similar lake histories, is fairly clear evidence that younger ocean-age fish have higher fecundity than older ocean-age sockeye of the same size. The rather consistent difference between 2- and 3-ocean-age fish would also indicate that the ocean environment is relatively stable as the two groups were not at sea during identical years.

If we now turn the analysis around and note the egg counts for 3- and 4-fresh-water-age fish with identical ocean histories that spend 2 and 3 summers in fresh water, the difference in fecundity is neither consistent nor significant. This could be interpreted to mean that fecundity does not differ between fish of 3 and 4 fresh-water ages, but since there are obvious differences between year classes, owing probably to lake conditions, such a conclusion is not fully warranted by these data. What is required are data over a sufficiently long period to discount these fresh-water environmental effects.

RELATION OF EGG SIZE TO EGG NUMBER

Surprisingly few records have been publish on actual size of ova of Salmonidae, investigat being content to speak of size in a purely compa tive sense. For instance, Belding et al. (19 p. 214) say—

> In general the size of the egg depends upon the size the parent salmon, the larger specimens producing larger egg. Also, the size of the egg varies with the mon of the different rivers. The material used in study permits its division into two classes, large and sm eggs. There is no relationship between the size of egg and the length of the incubation period.

Gilbert (1915, p. 57) also used only a compa tive measure of size. He says in speaking British Columbia sockeye,

> A similar difference, but even more pronounced, is fou among certain lots of eggs collected by Mr. Stone Smith Inlet, those from Quey Creek being markedly sma than those from the Gelulch and Delelah Rivers. It quired 74 Quey Creek eggs to fill a tube which would h only 38 from the Gelulch and the Delelah.

Perhaps the chief reason for this lack of data size of ova is that the salmon taken by t commercial fishery are in various stages of e maturation. Thus, at Karluk River many of t sockeye taken in the fishery may not spawn for least another month. This is reflected in t weight of sockeye eggs at Karluk ranging fr .03 to .095 grams (fig. 4).

The same late maturation is found in t Atlantic salmon. Speaking of *S. salar* in Norw Dahl and Sømme (1944, p. 39) say—

> In the grilse, which have spent more than a year in sea, the GW/TW [ratio of gonad weight to total weight still practically in the same undeveloped stage in early part of the season. A gradual development in relative size of the sexual organs asserts itself as the fi ing season advances, but the main growth towards mat ity takes place after the fish have entered the rivers.

They agree with Belding et al. that the in vidual egg size is partially dependent on fish si saying (op. cit., p. 22), "It is a well known fa that in large salmon the ovaria as well as t single ova are larger than in salmon of small size

Egg size is regarded by Svärdson (1949, p. 12 as resulting from natural selection. He states

> Summing up it can be said that the evidence now hand shows that competition among fry gives the lar

fry better survival chances. A selection pressure in favour of large eggs therefore certainly exists and this selection must work until the eggs are so few that no noteworthy competition for food exists among the fry.

While we must agree that larger fry generally have better survival rates, the reason given by Svärdson—intraspecific competition—may sometimes have little bearing on the matter; undoubtedly, there are other important factors. For instance, Robertson (1922) has pointed out that the race of small-sized sockeye salmon that spawns in Harrison Rapids, a tributary of the Fraser River, produces larger eggs than the other races of sockeye in the Fraser. This may be related to the fact that this is one of the few races of sockeye in which the young go to sea as fry, since large, vigorous fry would be required to survive in sufficient numbers to maintain the population.

It should be noted, moreover, that among the Pacific salmons (table 2) the smallest eggs are found in the sockeye which normally spend the longest time in fresh water. Size can be attained only by the sacrifice of number. In each ecological situation there is some point at which, on the average, the forces favoring size are exactly balanced by those favoring number. This point must vary between river systems, tending to produce genetic variation between populations for egg size and number.

TABLE 2.—*Size and weight of eggs and fry of certain North American Salmonidae*

[Asterisk (*) indicates diameter calculated from volumetric measure by Von Bayer conversion table]

Species and area	Eggs		Sac fry		Fry after yolk is absorbed		Authority
	Diameter	Weight	Length	Weight	Length	Weight	
	Mm.	*Gm.*	*Mm.*	*Gm.*	*Mm.*	*Gm.*	
Oncorhynchus:							
tshawytscha:							
Washington				0.520		0.509	Chapman (1938).
Columbia R.					35–40		Rich (1920).
Oregon	*6.3						Brice (1898).
Area not recorded	*7.8						Bower (1910).
Sacramento R., Calif.	*7.9						Stone (1897).
Do.					35–40		Rich (1920).
keta:							
Area not recorded					30–40	0.24–.62	Kobayashi (1953).
Hokkaido, Japan	*7.4	0.232					Watanabe (1956).
kisutch:							
Green R., Wash.						0.284	Chapman (1938).
Lakes in Montana	*8.4						Beal (1955).
Scott Creek, Calif.	*7.2						Shapovalov and Taft (1954).
gorbuscha:							
Sashin Creek, S. E. Alaska					971–1800	per pint	Skud (1955).
McClinton Cr., B. C.					32–38	ca 0.3	Pritchard (1944).
nerka:							
Yes Bay, Alaska	*6.3						Bower (1910).
Baker R., Wash.						0.192	Chapman (1938).
Salmo:							
salar:							
Rivers in Norway	5.3–7.0	0.1–.2					Dahl (1917).
Gaspe, P. Q.	6.8	0.200	17.4	0.180			Vladykov (1954).
Morell R., P. E. I.			17.7	0.141	27.5	0.057	Belding and Hyde (1932).
Nova Scotia			18.1	0.133	26.7	0.124	Do.
New Brunswick			18.8	0.146	27.9	0.144	Do.
Pollitt R., N. B.	5.4	0.090	16.0	0.110			Vladykov (1954).
Area not recorded	*6.1						Brice (1898).
s. sebago: Area not recorded	*6.6						Do.
gairdneri:							
Area not recorded	5.1						Do.
Scott Cr., Calif.	*5.5						Shapovalov and Taft (1954).
g. aqua-bonita: Cottonwood L., Calif.			15.0				Curtis (1935).
trutta:							
Area not recorded	*4.2						Brice (1898).
Madison R., Mont.	4.94						Brown and Kamp (1942).
clarki: Henrys L., Idaho	4.3–5.1						Irving (1955).
c. lewisi: Yellowstone R.	*4.5						Lord (1930).
Cristivomer:							
namaycush:							
Baldwins Mills, P. Q.	5.8	0.125	16.2	0.080			Vladykov (1954).
Twin Mountain, N. H.	5.7	0.125	19.1	0.075			Do.
Lake Superior	4.9–5.4						Eschmeyer (1955).
Seneca L., N. Y.	*5.2						Royce (1951).
Adirondack Lakes, N. Y.	*5.5–5.6						Do.
Northville, Mich.	*5.4						Bower (1910).
Area not recorded	*5.8						Brice (1898).
Salvelinus:							
alpinus: Area not recorded	5.0						Vladykov (1933).
aureolus: New Hampton, N. H.	4.7	0.050	17.1	0.055			Vladykov (1954).
fontinalis:							
L. Jacques-Cartier, P. Q.	4.4	0.040	15.0	0.033			Do.
New Hampton, N. H.	4.0	0.040	13.9	0.040			Do.
Vermont	*4.6						Bower (1910).
Area not recorded	*4.2						Brice (1898).

The data given in table 2 are from several sources. Undoubtedly exhaustive search of the literature would reveal more data on the subject; however, these suffice to give a general picture. Because data on ova size are missing or very scanty for several species we have included length and weight of sac fry and free-swimming fry.

Egg size, in general, is correlated with the average size of the species. Thus *Oncorhynchus tshawytscha*, the largest species, has the largest ova. This is, however, only a generalization. It may be noted that the fry of the small pink salmon, *O. gorbuscha*, are larger than those of the Atlantic salmon, *Salmo salar*. That is, the tendency toward large eggs and fry appears to be a characteristic of the genus *Oncorhynchus*. Because of the scarcity of data from actual measurement of diameters of mature eggs, it is felt that the scattered material brought together in table 2 cannot be wholly relied on to give a true picture of egg size. However, corroborative evidence can be obtained by an indirect method.

In figure 6 (data from appendix table 4), the average number of eggs is plotted against the average weight of the females for each speci (See also appendix tables 1, 2, and 3 for detai information on egg numbers, by species a locality.) Obviously the data fall into t general groups: fluvial anadromous *Oncorhynch* which show a low number of eggs for their weig and lacustrine anadromous sockeye and memb of the other 3 genera, which show a large numl of eggs for their weight. That this difference egg number for comparable weights is not due a difference in the shape of the fish is indicat by the very close correspondence between t length-weight relation for all of the genera (fig. data from appendix table 5).

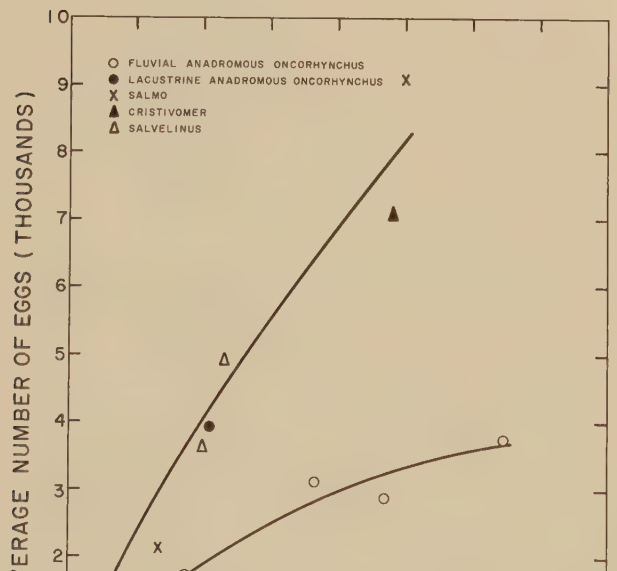

FIGURE 6.—Relation, by species, of average egg number to average weight. (Data from appendix table 4.)

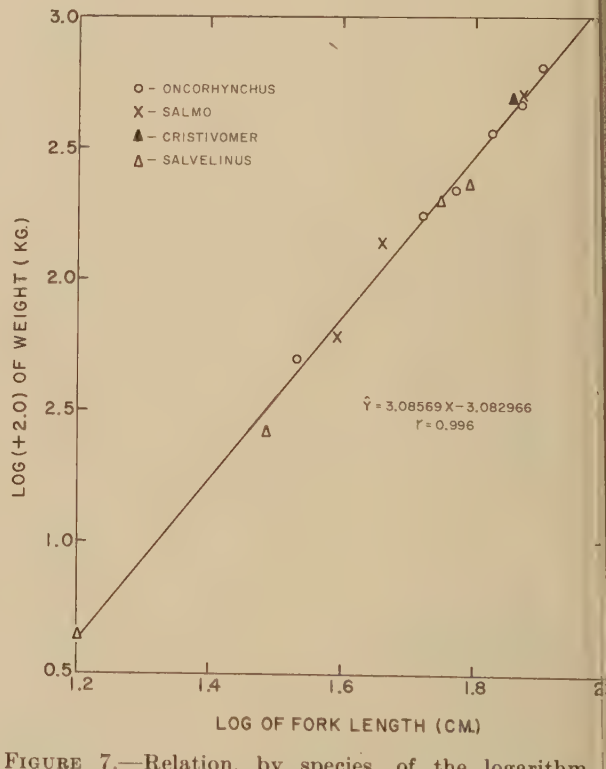

FIGURE 7.—Relation, by species, of the logarithm mean weight to the logarithm of mean fork lengt (Data from appendix table 5.)

It must therefore be concluded that the low egg number in the fluvial anadromous species *Oncorhynchus* can be due only to one of tw causes: either the eggs form a smaller percentag of the total weight of the fish or the eggs a considerably larger. Despite the paucity available information, the true cause of th lower egg number in these species can be conf

dently ascribed to egg size if we consider the data on weight of fry in conjunction with that of egg diameter (see appendix table 6). Thus, the sac fry of *O. tshawytscha* weighed 2.9 times the upper limit given for *Salmo salar*.

There is general agreement that, within the genus *Oncorhynchus*, the largest eggs are found in *tshawytscha* and the smallest in *nerka*. O'Malley (1920) gives the following number of eggs of each species required to fill a hatchery basket:

Species:	*Thousands of eggs*
O. tshawytscha	20–30
O. kisutch	30–35
O. keta	33–38
O. gorbuscha	40–50
O. nerka	50–60

Bean (1893, p. 30) says of the pink salmon, *O. gorbuscha*, "The eggs are larger than those of the red salmon [*O. nerka*], but smaller than king salmon [*O. tshawytscha*] eggs and not so bright red."

It is not surprising that there is some disagreement concerning the relative size of the eggs of *kisutch*, *keta*, and *gorbuscha* since, as we have seen, there is considerable difference between localities in regard to average number within the same species. Only accurate measurements of fully mature eggs from several localities, preserved in the same manner, can be relied upon to show the size ranges in eggs of the various species.

RELATION OF EGG NUMBER TO LATITUDE

In order to determine whether there is any relation between fecundity and latitude we have constructed table 3, showing the average fork length and egg number for species of *Oncorhynchus* arranged geographically from south to north. The averages are shown in figure 8 with the southernmost locality for each species in black. The egg number of four of the species is higher than expected for the average length in the most southern locality.

If further research should prove that there is a valid tendency for higher fecundity toward the south, this may possibly be ascribed to the difference in growth rates. This follows because the average age at maturity of all of the species (except *gorbuscha*) tends to increase toward the north. We have already shown that at Karluk the sockeye spending 2 years at sea have a higher fecundity than sockeye of the same length spending 3 years at sea.

TABLE 3.—*Egg number and fork length in species of* Oncorhynchus, *arranged geographically from south to north*

[Includes only samples of more than 20 fish]

Species and area	Average number of eggs	Fork length	Number of fish
		Cm.	
nerka:			
Fraser R., B. C.	4,048	58.33	463
Namu, B. C.	3,264	57.2	33
Skeena R., B. C.	3,432	59.50	276
Nass R., B. C.	3,461	66.5	35
Karluk R., Alaska	3,277	59.59	451
kisutch:[1]			
Fraser R., B. C.	3,152	65.3	48
Namu, B. C.	3,002	69.85	21
gorbuscha:			
Fraser R., B. C.	1,755	51.8	48
Namu, B. C.	1,841	53.6	41
McClinton Cr., B. C.	1,733	52.6	536
Sashin Cr., S. E. Alaska	2,074	54.6	77
keta:			
Fraser R., B. C.	2,943	73.9	51
Namu, B. C.	2,760	73.9	21
tshawytscha:			
Sacramento R., Calif.	5,449	83.71	108
Klamath R., Calif.	3,753	81.35	105
Cowichan R., B. C.	3,885	86.4	25

[1] Scott Creek omitted, as averages (appendix table 1) were read from regression curve.

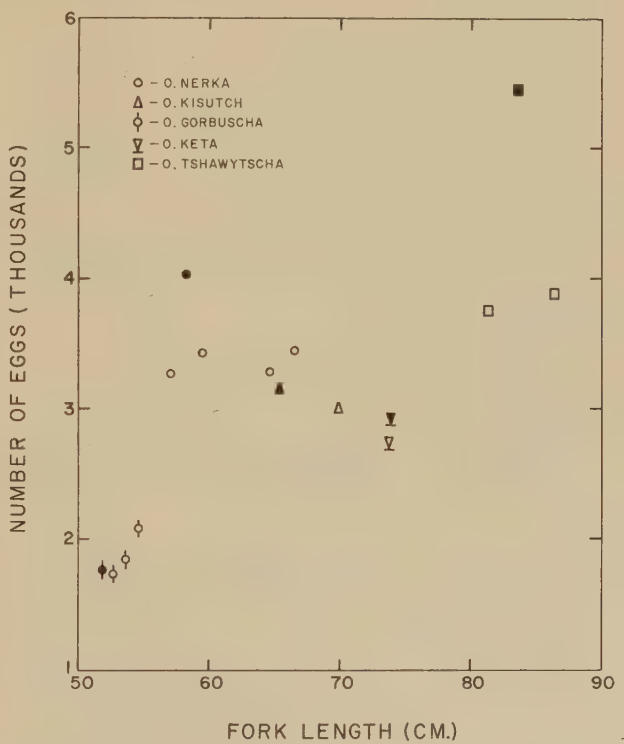

FIGURE 8.—Relation of mean egg number to mean fork length in species of *Oncorhynchus*, by locality. Southernmost localities are shown in solid black for each species.

SUMMARY

The data show differences in fecundity between populations of the same species of salmon for different localities—the best examples being the king salmon, *Oncorhynchus tshawytscha*, of the Sacramento and Klamath Rivers; the sockeye salmon, *O. nerka*, of the Skeena River system; and the chum salmon, *O. keta*, of Japan.

The number of eggs shows a linear relation with the logarithm of fork length; but for *Oncorhynchus*, in which the size range of the mature adults is slight, the regression of egg number on fork length may more conveniently be treated as linear.

There is an annual variation in fecundity. Owing possibly to the short life history of the pink salmon, this variation is pronounced in that species. The annual differences in fecundity of pink salmon are shown by covariance analysis to be negatively associated with sea temperature for a Queen Charlotte Island population.

The number of eggs in the left and in the right ovary differs in some species, the left ovary usual having the larger number; but this will va with the individual fish. This disparity betwe the two ovaries in egg number is apparently d to one ovary exceeding the other in length becau of crowding of the small posterior end of the bo cavity by the intestine.

Fecundity in sockeye salmon was not shown be affected by length of sojourn in fresh wat prior to entering the sea. However, socke spending 2 years at sea mature more eggs th sockeye of the same size with 3 years of sea li

The four species of fluvial anadromous *O corhynchus* have larger eggs than the sockey *O. nerka*, or species of the other genera.

There is a suggestion of lower fecundity fro south to north in *Oncorhynchus* (except in *gorbuscha*). This may be caused by a higher a at maturity, and therefore slower growth rat from south to north.

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APPENDIX

APPENDIX TABLE 1.—*Number of eggs at maturity in North American Salmonidae of the genus* Oncorhynchus

Species and area	Average number of eggs	Sampling					Number of eggs per kilogram	Authority
		Number in sample	Year	Age	Average fork length	Average weight of fish		
hawytscha:					*Cm.*	*Kg.*		
Sacramento R., Calif.	7,422	50	1922		92.4			McGregor (1923a).
Do	3,423	20	1950		75.4	4.72	725	Wales and Coots (1955).
Do	3,948	20	1951		80.0	6.40	617	Do.
Do	3,888	18	1952		72.9	4.58	849	Do.
Fort Bragg, Calif.	5,034	53	1922		80.8			McGregor (1923b).
Klamath R., Calif.	3,419	24	1920	4	78.5	6.175	554	Snyder (1921).
Do	4,297	5	1920	5	88.0	8.664	496	Do.
Do	2,648	3	1921	3	64.7			McGregor (1922).
Do	3,504	29	1921	4	75.2			Do.
Do	4,364	27	1921	5	89.8			Do.
Do	4,270	6	1921	6	95.5			Do.
Do	3,570	[1] 29	1920		80.1	6.604	541	Snyder (1921).
Do	3,892	[1] 65	1921		82.7			McGregor (1922).
Do	3,413	11	1922		76.7			McGregor (1923b).
Fraser R., B. C.	4,944	12	1934		87.1	9.843	502	Foerster and Pritchard (1936).
Cowichan R., B. C.	3,885	25	1935		86.4	8.346	465	Do.
Namu, B. C.	8,426	11	1934		103.4	16.148	522	Do.
Kamchatka	8,154							Kuznetzow (1928).
ta:								
Fraser R., B. C.	2,943	51	1934		73.9	4.58	643	Foerster and Pritchard (1936).
Nile Cr., B. C.	2,726	47						Neave (1953).
Namu, B. C.	2,760	21	1934		73.9	4.94	559	Foerster and Pritchard (1936).
Hooknose Cr., B. C.	2,254	114						Neave (1953).
Port John Cr.	2,107	94	1947–48					Hunter (1948, 1949).
Hokkaido, Japan	2,625	109			58.8			Eguchi et al. (1954).
Do	3,153	40	1940–43	3.5	61.0	3.84	821	Watanabe (1956).
South Kurile, Japan	2,000	134			56.6			Eguchi et al. (1954).
Siberia (summer)	2,498							Kuznetzow (1928).
Siberia (autumn)	4,302							Do.
Kamchatka	2,544							Do.
sutch:								
Scott Cr., Calif.	[2] 2,500	65	1935–36		65.3			Shapovalov and Taft (1954).
Montana lakes	567	37			34.0	0.50	1,136	Beal (1955).
Fraser R., B. C.	3,152	48	1934		65.3	3.45	914	Foerster and Pritchard (1936).
Cowichan R., B. C.	2,329							Neave (1948).
Port John Cr., B. C.	2,313	3	1947					Hunter (1949).
Namu, B. C.	3,002	21	1934		69.8	4.13	727	Foerster and Pritchard (1936).
Nile Cr., B. C.	2,310	[3]	1945–49					Wickett (1951).
Kamchatka	4,883							Kuznetzow (1928).
rbuscha:								
Fraser R., B. C.	1,755	48	1934	2	51.8	1.72	1,020	Foerster and Pritchard (1936).
Morrison Cr., B. C.	1,779	38	1943	2				Neave (1953).
Do	1,862	27	1945	2				Do.
Port John Cr., B. C.	1,520	38	1947	2				Do.
Do	1,320	57	1947–48	2				Hunter (1948, 1949).
Do	1,593	20	1950	2				Neave (1953).
Namu, B. C.	1,841	41	1934	2	53.6	1.86	990	Foerster and Pritchard (1936).
McClinton Cr., B. C.	1,535	97	1930	2	51.1			Foerster and Pritchard (1941).
Do	1,538	[4] 91	1930	2		1.64	938	Do.
Do	1,758	73	1932	2	54.0			Do.
Do	1,804	165	1934	2	53.0	1.76	1,025	Do.
Do	1,899	91	1936	2	53.0			Do.
Do	1,899	[4] 90	1936	2		1.70	1,117	Do.
Do	1,698	40	1938	2	52.7	1.81	938	Do.
Do	1,619	70	1940	2	51.6	1.63	993	Do.
Do	1,733	[1] 536	1930–40	2	52.6			Do.
Do	1,599	[1] [4] 456	1930–40	2		1.71	935	Do.
Sashin Cr., S. E. Alaska	2,074	77	1951	2	54.6			Hanavan and Skud (1954).
Siberia	1,192	52	Even	2		1.12	1,069	Kuznetzow (1928).
Do	1,913	73	Odd	2		1.82	1,054	Do.
rka:								
Cultus L., B. C.	4,310	46	1932		58.5			Foerster and Pritchard (1941).
Do	4,267	[4] 43	1932			1.95	2,188	Do.
Do	3,796	47	1933		56.5	1.70	2,233	Do.
Do	4,282	75	1934		59.0	2.00	2,141	Do.
Do	4,067	55	1935		59.0	2.05	1,984	Do.
Do	3,864	35	1937		56.0			Do.
Do	3,864	[4] 36	1937			1.75	2,208	Do.
Do	4,246	47	1938		58.5			Do.
Do	4,248	[4] 32	1938			2.05	2,072	Do.
Do.[5]	3,800	112	1933		57.0	1.95	1,949	Do.
Fraser R., B. C.	4,180	46	1934		63.0	3.04	1,375	Foerster and Pritchard (1936).
Namu, B. C.	3,264	33	1934		57.2	2.09	1,562	Do.
Port John Cr., B. C.	2,511	3	1948					Hunter (1949).
Lakelse L., Skeena R.	3,888	24	1939		59.6			Aro and Broadhead (1950).
Do	3,860	22	1948		59.0			Do.
Do	3,699	41	1949		58.1			Do.
Babine L., Skeena R., B. C.	3,281	59	1946		60.9			Withler (1950).
Do	3,187	73	1947		59.1			Do.
Do	3,353	57	1949		59.7			Do.
Nass R., B. C.	3,461	35	1934		66.5	3.08	1,124	Foerster and Pritchard (1936).

See footnotes at end of table.

APPENDIX TABLE 1.—*Number of eggs at maturity in North American Salmonidae of the genus* Oncorhynchus—Contin

Species and area	Average number of eggs	Sampling					Number of eggs per kilogram	Authority
		Number in sample	Year	Age	Average fork length	Average weight of fish		
					Cm.	*Kg.*		
nerka:—Continued								
Karluk R., Alaska	3,691	40	1926		60.8			Gilbert and Rich (1927).
Do	3,305	24	1938	5_3	58.7			This report.
Do	3,082	9	1938	6_3	63.2			Do.
Do	2,909	10	1938	6_4	57.6			Do.
Do	3,190	[14] 46	1938	5–7	59.6			Do.
Do	2,548	36	1939	5_3	54.8			Do.
Do	3,049	58	1939	6_3	60.7			Do.
Do	2,805	13	1939	7_4	59.5			Do.
Do	2,842	[14] 117	1939	4–7	58.3			Do.
Do	3,421	80	1940	5_3	60.0			Do.
Do	2,926	23	1940	6_3	60.0			Do.
Do	3,549	25	1940	6_4	60.0			Do.
Do	3,357	[14] 135	1940	4–7	60.0			Do.
Do	3,708	45	1941	5_3	60.0			Do.
Do	3,006	20	1941	6_3	60.0			Do.
Do	3,668	36	1941	6_4	60.0			Do.
Do	3,160	11	1941	7_4	60.0			Do.
Do	3,521	[14] 113	1941	4–7	60.0			Do.
Kamchatka	3,763							Kuznetzow (1928).
n. kennerlyi:								
L. Washington, Wash	452±51	23	1938		[6] 27.3			Scattergood (1949).
Kootenay L., B. C	368	2	1898		[7] 22.9			Do.
California reservoir	479	626	1943					Curtis and Fraser (1948).

[1] Summary.
[2] Values read from published regression curve.
[3] 3 to 8 specimens per year.
[4] Partial duplication of fish in previous total or totals.
[5] Marked Cultus Lake *O. nerka* caught outside of Fraser River.
[6] Standard length of 103 females converted to fork length by factor 1.1.
[7] Standard length of 5 females converted to fork length by factor 1.1.

APPENDIX TABLE 2.—*Number of eggs at maturity in North American Salmonidae of the genus* Salmo

Species and area	Average number of eggs	Sampling					Number of eggs per kilogram	Authority
		Number in sample	Year	Age	Average fork length	Average weight of fish		
					Cm.	*Kg.*		
salar:								
Miramichi R., Canada	7,678	163		2 sea	[1] 71.4	4.26	1,802	Belding (1940).
Gulf of St. Lawrence	9,409	340		2 sea	[1] 74.8	5.07	1,856	Do.
Do	13,883	15		3 sea	[1] 86.7	8.68	1,594	Do.
Do	12,313	16		([2])	[1] 83.6	7.57	1,627	Do.
gairdneri:								
Scott Cr., Calif.[3]	2,400	537	1932–33		40.0			Shapovalov and Taft (1954).
Do	3,900				50.0			Do.
Do	5,600				60.0			Do.
Do	7,600				70.0			Do.
g. aqua-bonita:								
Cottonwood Lakes, Calif	326	450			20.0			Curtis (1935).
Do	765				30.0			Do.
Do	1,102				37.5			Do.
clarki:								
Henrys L., Idaho	1,577	10	1953		[4] 31.9	0.573	2,752	Irving (1955).
Do	1,914	10	1953		[4] 40.8	1.180	1,622	Do.
Do	2,930	10	1953		[4] 51.8	2.394	1,224	Do.
c. lewisi: Yellowstone R	1,113	104						Lord (1930).
c. henshawi:								
Blue L., Calif.[3]	1,100	55	1941	([5])	35.0	0.33	3,333	Calhoun (1944).
Do	1,750		1941	([5])	40.0	0.50	3,500	Do.
Do.[3]	750	38	1941	([2])	35.0	0.30	2,500	Do.
Do	900		1941	([2])	40.0	0.44	2,045	Do.
Heenan L., Calif	[6] 3,560	214	1940					Smith, O. (1947).
Do	[6] 2,594	310	1941					Do.
Do	[6] 2,508	320	1942					Do.
trutta:								
Madison R., Mont	1,238	1	1936	2	[4] 37.1	0.51	2,427	Brown and Kamp (1942).
Do	1,383	18	1936	3	[4] 37.6	0.55	2,515	Do.
Do	1,164	14	1936	4	[4] 40.7	0.66	1,764	Do.
Do	1,279	4	1936	5	[4] 41.4	0.68	1,881	Do.
Convict L., Calif	1,061	14	1952					Nielson (1953).
Michigan streams	1,208	78			34.0			Cooper (1953).

[1] These values from weight-length regression of fig. 6.
[2] Previously spawned.
[3] Readings from published regression curves.
[4] Standard length converted to fork length by factor 1.1.
[5] First spawning.
[6] Eggs stripped by hatchery.

APPENDIX TABLE 3.—*Number of eggs at maturity in North American Salmonidae of the genera* Cristivomer *and* Salvelinus

Species and area	Average number of eggs	Sampling					Number of eggs per kilogram	Authority
		Number in sample	Year	Age	Average fork length	Average weight of fish		
Cristivomer:								
namaycush:					*Cm.*	*Kg.*		
Lake Ontario	7,943	25	1927		72.7	5.00	1,589	Dymond (1928).
Lake Superior	3,383	9	1951–53		[1] 60.7	2.81	1,204	Eschmeyer (1955).
Do	4,253	15	1951–53		[1] 65.4	3.36	1,266	Do.
Do	4,995	13	1951–53		[1] 70.4	4.26	1,173	Do.
Do	8,667	17	1951–53		[1] 75.3	5.26	1,648	Do.
Do	8,881	8	1951–53		[1] 78.5	6.31	1,408	Do.
Do	11,603	6	1951–53		[1] 83.2	7.48	1,551	Do.
Do	13,836	2	1951–53		[1] 87.9	8.75	1,581	Do.
Do	11,789	2	1951–53		[1] 93.9			Do.
Do		[2] 72					1,424	Do.
n. siscowet: Lake Superior	4,387	12	1950–54		[1] 59.2	4.34	1,011	Do.
Salvelinus:								
alpinus:								
Baffin Island	3,589	23	1950–51	13–22	56.0			Grainger (1953).
Do	3,645	[3] 21	1950–51	13–22		2.00	1,822	Do.
Ungava Bay	2,726	6	1951	7–9	41.2			Do.
Lakes in Sweden	909	211	1945–48		30.6	0.26		Mär (1949).
Do	1,313	51	1949		31.4			Mär (1950).
Do	1,443	[3] 42	1949			0.26		Do.
malma: Clark's Fork R., Mont	4,927	28	1950		61.9	2.31	2,133	Brunson (1952).
fontinalis:								
New Jersey (domestic)	1,183	53		([4])	29.9			Hayford and Embody (1930).
Do	1,414	20		([5])	31.4			Do.
Michigan streams	254	239			[1] 14.4			Cooper (1953).
Wyoming beaver pond	148	2	1952		12.70	0.0215	6,907	Allen (1956).
Do	191	5	1952		14.44	0.0316	6,032	Do.
Do	275	5	1952		16.82	0.0506	5,435	Do.
Do	376	2	1952		19.65	0.0835	4,509	Do.
Laurentides Park, P. Q	399	77			22.3			Vladykov and Legendre (1940).
Various (wild)	[6] 410	29			20.3			Smith (1947).
Do	[6] 640				25.4			Do.
Do	[6] 950				27.9			Do.
Do	[6] 1,400				35.6			Do.

[1] Total length converted to fork length by factor 0.92.
[2] Summary.
[3] Partial duplication of fish in previous total or totals.
[4] First spawning.
[5] Previously spawned.
[6] Values read from published regression curve.

APPENDIX TABLE 4.—*Summary of number of eggs by size of fish for North American Salmonidae*

Species	All specimens		Specimens with length data				Specimens with weight and length data			
	Average number of eggs	Number of fish	Average fork length	Mean number of eggs	Average number of eggs per centimeter	Number of fish	Average weight of fish	Average number of eggs	Average number of eggs per kilogram	Number of fish
Oncorhynchus:			*Cm.*				*Kg.*			
tshawytscha	4,772	314	83.46	4,772	57.2	314				
			79.26	3,759	47.4	207	6.465	3,759	581	207
keta	2,546	233	73.90	2,890	39.1	72	4.685	2,890	617	72
kisutch	2,801	137	66.01	2,812	42.6	134				
			66.68	3,106	46.6	69	3.657	3,106	849	69
kisutch [1]	567	37	34.00	567	17.7	37	0.499	567	1,136	37
gorbuscha	1,765	825	52.82	1,778	33.7	702				
			52.61	1,754	33.3	364	1.746	1,754	1,005	364
nerka	3,597	1,262	59.24	3,600	60.8	1,258	2.121	3,946	1,860	514
			59.11	3,896	65.9	403	2.178	3,896	1,789	403
n. kennerlyi	[1] 478	651	26.95	445	16.5	25				
Salmo:										
salar	9,092	534	74.36	9,092	122.3	534	4.999	9,092	1,819	534
gairdneri [2]	[3] 5,541	537	[4] 59.00	(5,541)	93.9	562				
clarki [1]	2,140	30	45.65	2,140	46.9	30	1.382	2,140	1,548	30
c. lewisi	1,113	104								
c. henshawi	2,806	844								
trutta	1,233	115	35.66	1,233	34.6	115				
			39.17	1,258	32.8	37	0.605	1,285	2,124	37
Cristivomer: namaycush	7,186	97	72.03	7,089	98.4	95	4.825	7,089	1,469	95
Salvelinus:										
alpinus [2]	3,410	29	52.94	3,410	64.4	29				
			56.00	3,589	64.1	23	2.000	3,645	1,822	21
alpinus [5]	988	262	30.76	988	32.1	262	0.260	998	3,838	253
malma [1]	4,927	28	61.90	4,927	79.6	28	2.310	4,927	2,133	28
fontinalis [1]	461	403	18.84	461	24.5	403				
			15.79	241	15.3	14	0.044	241	5,477	14

[1] In fresh water.
[2] Anadromous.
[3] Calculated from egg volumes (Shapovalov and Taft, 1954, table A–17).
[4] Values from regression curve.
[5] In Swedish lakes.

APPENDIX TABLE 5.—*Summary of length-weight data on North American Salmonidae*

[A=anadromous; F=fresh water]

Species	Habitat	Average weight	Average fork length	Number in sample	Logarithm	
					Average weight+2.0 Y	Average length X
		Kg.	*Cm.*			
Oncorhynchus:						
tshawytscha	A	6.465	79.26	207	2.8106	1.
keta	A	4.685	73.90	72	2.6707	1.
kisutch	A	3.657	66.68	69	2.5631	1.
kisutch	F	0.499	34.00	37	1.6981	1.
gorbuscha	A	1.746	52.61	364	2.2420	1.
nerka	A	2.178	59.11	403	2.3381	1.
Salmo:						
salar	A	4.999	74.36	534	2.6989	1.
clarki	F	1.382	45.65	30	2.1405	1.
trutta	F	0.605	39.17	37	1.7818	1.
Cristivomer: namaycush	F	4.825	72.03	95	2.6835	1.
Salvelinus:						
alpinus	A	2.000	56.00	21	2.3010	1.
alpinus	F	0.260	30.76	253	1.4150	1.
malma	F	2.310	61.90	28	2.3636	1.
fontinalis	F	0.044	15.79	14	0.6435	1.

APPENDIX TABLE 6.—*Summary of various measures of egg size in North American Salmonidae*

Group and species	Eggs per cm. of fish	Eggs per kg. of fish	Egg diameter		Weight of sac fry	Weight of with yo absorbe
			Measured	Calculated		
Oncorhynchus:			*Mm.*	*Mm.*	*Gm.*	*Gm.*
Fluvial anadromous:						
tshawytscha	47	581		6.3–7.9	0.520	0
keta	39	617		7.4		0.24–
kisutch	47	849		7.2		0
gorbuscha	33	1,005				Ca.
Lacustrine anadromous: *nerka*	66	1,789		6.3		0
Fresh water: *kisutch*	18	1,136		8.4		
Salmo:						
Fluvial anadromous:						
salar	122	1,819	5.4–6.8	6.1	0.110–0.180	0.057–0
gairdneri	94		5.1	5.5		
Fresh water:						
salar sebago				6.6		
clarki	47	1,548	4.3–5.1			
clarki lewisi				4.5		
trutta	33	2,124	4.9	4.2		
Cristivomer:						
Fresh water: *namaycush*	98	1,469	4.9–5.8	5.2–5.8	0.075–0.080	
Salvelinus:						
Anadromous: *alpinus*	64	1,822	5.0			
Fresh water:						
alpinus (Sweden)	32	3,838				
aureolus			4.7		0.055	
malma	80	2,133				
fontinalis [1]	15	5,477	4.0–4.4	4.2–4.6	0.033–0.040	

[1] The small sample available contained only small fish so that these figures are not believed to be representative for eggs per centimeter or per kilogr